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Renomaera patricki gen. et sp. nov. (Amphipoda, Hadzioidea, Maeridae) described from the seamount in the western Pacific, with a test of monophyly of Maeridae Krapp-Schickel, 2008

Zhong-Li Sha[1,2,3,4], Yan-Rong Wang[1,4]

1 *Laboratory of Marine Organism Taxonomy and Phylogeny, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China*
2 *Laboratory for Marine Biology and Biotechnology, Qingdao Marine Science and Technology Center, Qingdao 266237, China*
3 *Shandong Province Key Laboratory of Experimental Marine Biology, Institute of Oceanology, Chinese Academy of Sciences, Qingdao, 266071 China*
4 *College of Biological Sciences, University of Chinese Academy of Sciences, Beijing 100049, China*

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Corresponding author: Yan-Rong Wang (wangyr@qdio.ac.cn)

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Abstract

A new genus, *Renomaera* **gen. nov.**, belonging to the family Maeridae Krapp-Schickel, 2008, is erected for a new species, *Renomaera patricki* **sp. nov.**, based on a specimen collected from seamounts near the Mariana Trench in the western Pacific. *Renomaera* **gen. nov.** is unique within the family in having the following combination of characters: a mandible lacking a molar, the inner plate of maxilla 1 with only one apical seta, reduced inner and outer plates of the maxilliped, and the inner ramus of uropod 3 bearing long plumose setae. Phylogenetic analyses based on one mitochondrial gene (cytochrome c oxidase subunit I (COI)) and two nuclear genes (histone H3 (H3) and 28S ribosomal RNA (28S rRNA)), using maximum likelihood (ML) and Bayesian inference (BI), revealed that Maeridae is non-monophyletic and that the *Maera* clade is also non-monophyletic.

Key Words

Deep sea, morphology, new genus, phylogenetics, taxonomy

Introduction

The amphipod family Maeridae Krapp-Schickel, 2008, encompasses 414 species across 49 genera (Horton et al. 2025) and inhabits depths ranging from the intertidal zone to over 7000 m (e.g., Birstein and Vinogradova 1960; Hughes 2016). Species from at least ten genera have been recorded at depths exceeding 200 m (Barnard 1932; Pirlot 1934; Nicholls 1938; Birstein and Vinogradova 1960; Lowry and Bullock 1976; Mukai 1979; Andres 1984; Krapp-Schickel and Vader 2013; Corbari and Sorbe 2015; SOSA et al. 2024). Among these, two genera, *Bathyceradocus* Pirlot, 1934, and *Papuadocus* Corbari & Sorbe, 2015, are associated with sunken wood. *Cuniculomaera grata* Tandberg & Jażdżewska, 2024, has been identified as a burrow constructor at depths greater than 3000 m (Brandt et al. 2023), and *Huonella huonensis* Hughes, 2016, was discovered on a seamount off Tasmania (Hughes 2016).

During a biodiversity survey of seamounts near the Mariana Trench, a single maerid specimen was collected in association with a sponge (*Semperella* sp., Fig. 1). Detailed examination revealed that this specimen represents a new species, distinguished from all known maerid species by a unique set of characteristics. Consequently, a new genus is established to accommodate this species. Descriptions and illustrations of the species are provided herein.

Maeridae was previously classified within Melitidae Bousfield, 1973, and was established based on uropod 3 having subequal rami (Krapp-Schickel 2008). However, the monophyly of the family has not been conclusively demonstrated. To clarify phylogenetic relationships with-

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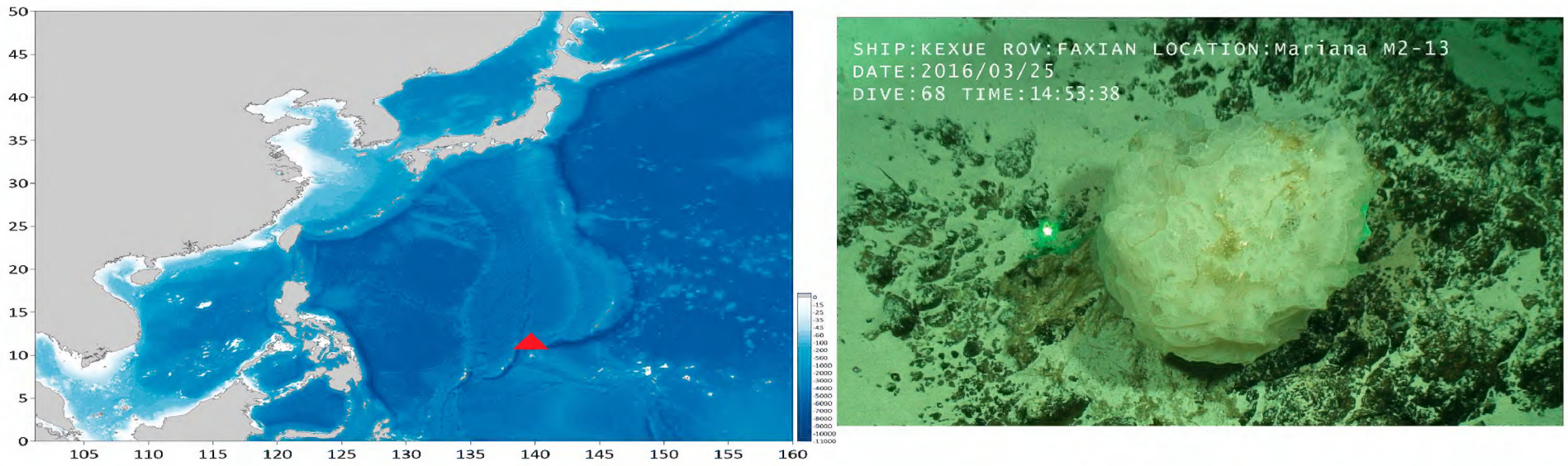

Figure 1. Left: map showing the location of the sampling site (red triangle) in the northwestern Pacific; right: *in situ* view showing the sponge collected with the holotype specimen.

in the superfamily Hadzioidea S. Karaman, 1943, we reconstructed a phylogeny using nuclear and mitochondrial DNA sequences.

Material and methods

Benthic animals were collected from a seamount located near the Mariana Trench (tentatively named M2 Seamount) in the western Pacific using the research vessel KEXUE with the remotely operated vehicle (ROV) FAXIAN. The amphipod specimen was sorted on board and fixed in 96% ethanol, then transferred to 75% ethanol in the laboratory for further study. External morphology and internal anatomy were examined, dissected, and photographed under a microscope (ZEISS Discovery V20). Line drawings were completed using Adobe Photoshop CS6 with a graphics tablet (Wacom PTH 851). Length measurement was made along the outline of the animal, from the anterior margin of the head to the posterior margin of the telson. The examined specimen is deposited in the Marine Biological Museum of the Chinese Academy of Sciences (**MBMCAS**), Qingdao, China.

Abbreviations used in Figs 3, 4: E1–3, epimera 1–3; U1–3, urosomites 1–3; A1 and A2, antennae 1 and 2; UL, upper lip; MdL and MdR, left and right mandibles; LL, lower lip; Mx1L and Mx1R, left and right maxillae 1; Mx2R, right maxilla 2; Mxp, left maxilliped; G1R and G2R, right gnathopods 1 and 2; P3R–P7R, right pereopods 3–7; U1R–U3R, uropods 1–3; T, telson.

Genomic DNA of *Renomaera patricki* gen. et sp. nov. was obtained from an intra-marsupial individual specimen held by the holotype female using Illumina HiSeq sequencing (approximately 10 G), and de novo genome assembly was performed using SPAdes version 4.0.0 (Bankevich et al. 2012). The cytochrome c oxidase subunit I (COI) sequence was obtained from the mitochondrial genome by BLAST (Camacho et al. 2009) and annotated using MITOS (Bernt et al. 2013). The 28S ribosomal RNA (28S rRNA) sequence was obtained using Barrnap version 0.9 (Seemann 2013), and the histone H3 (H3) sequence was obtained by BLAST. All sequences were deposited in GenBank (for accession numbers, see Suppl. material 1).

As for most maerid species, only one mitochondrial gene (COI) was available; therefore, two different data sets were used in this study. The first data set consisted of species for which sequences from two nuclear gene fragments (28S rRNA and H3) and one mitochondrial gene (COI) were available (see Suppl. material 1). This data set comprised a total of 22 species, including the new species, representing the families Maeridae, Melitidae, Nuuanuidae Lowry & Myers, 2013, Eriopisidae Lowry & Myers, 2013, Hadziidae Karaman, 1943, and Metacrangonyctidae Boutin & Messouli, 1988, with two species from Calliopiidae G.O. Sars, 1893, used as outgroup terminals (Suppl. material 1). The second data set consisted of species for which sequences from one nuclear gene (H3) and one mitochondrial gene (COI) were available. This data set comprised a total of 21 species, including the new species, within five families (Maeridae, Melitidae, Nuuanuidae, Eriopisidae, and Metacrangonyctidae), with two species from Calliopiidae used as outgroup terminals (Suppl. material 1).

The sequences obtained were aligned using MAFFT (Katoh and Standley 2013), and the 28S rRNA alignment was trimmed using trimAL (Capella-Gutiérrez et al. 2009). Resulting alignments were concatenated using SequenceMatrix 1.8 (Vaidya et al. 2011). The optimal model of evolution for each data set was determined using jModelTest 0.1.1 based on the Akaike information criterion (AIC) (Posada 2008).

Phylogenetic trees were constructed using both maximum likelihood (ML) and Bayesian inference (BI) methods. ML analyses were conducted online using W-IQ-TREE (http://iqtree.cibiv.univie.ac.at/) (Trifinopoulos et al. 2016), with clade support evaluated using 10,000 ML bootstrap replications. BI analyses were performed using MrBayes 3.2.7 (Huelsenbeck and Ronquist 2001) under the best partition model for 5 million Markov chain Monte Carlo (MCMC) generations, using four chains and a sampling frequency of 1000. The first 12,500 trees (25% of the total) were discarded as burn-in. The remaining 37,500 trees were used to calculate posterior probabilities (PP). Effective sample size (ESS) values for all sampling parameters were checked using Tracer v1.7 (Rambaut et al. 2018).

Systematic account

Order Amphipoda Latreille, 1816
Suborder Senticaudata Lowry & Myers, 2013
Infraorder Hadziida S. Karaman, 1943
Parvorder Hadziidira S. Karaman, 1932
Superfamily Hadzioidea S. Karaman, 1943
Family Maeridae Krapp-Schickel, 2008

Genus *Renomaera* gen. nov.

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Diagnosis. Head with rostrum. Eyes lacking. Antenna 1 longer than antenna 2, slender, accessory flagellum longer than peduncle. Mandible robust, incisor with large tooth laterally; left lacinia mobilis almost smooth distally, right lacinia mobilis absent; molar absent; palp article length 2>3>1, article 1 without distal tooth, article 3 not falciform. Maxilla 1 inner plate with one apical seta; palp two-articulate. Maxilla 2 inner plate with long setae on medial margin; outer plate with setae apically. Maxilliped inner and out plates reduced; palp with 4 articles, slender. Coxae shallow; coxa 4 not excavate posteriorly; gills on coxae 2–7; oostegites on pereonites 2–5. Both gnathopods similar, subchelate, palmar margin smooth. Pereopods with simple dactyli: pereopods 5–7 gradually increasing in length. Urosomites 1–2 with dorsomedian teeth. Uropods 1–2 rami with apical robust setae. Uropod 3 biramous and uniarticulate, rami subequal, with apical robust setae, outer ramus with long plumose setae. Telson deeply cleft.

Etymology. The genus is named in honor of the retired Professor Xianqiu Ren of the Institute of Oceanology, Chinese Academy of Sciences, for his great contributions to Chinese carcinology, combined with the family name Maeridae. The name is masculine in gender.

Remarks. The family Maeridae Krapp-Schickel, 2008, was distinguished from Melitidae Bousfield, 1973, by the morphology of uropod 3 and originally comprised three clades: the *Ceradocus* clade, the *Elasmopus* clade, and the *Maera* clade (Krapp-Schickel 2008). Subsequently, twenty-two additional genera have been included in Maeridae (e.g., Lowry and Hughes 2009; Lowry and Myers 2013; Corbari and Sorbe 2015; Hughes 2015, 2016; Ariyama 2018; SOSA et al. 2024). *Renomaera* gen. nov. clearly belongs to Maeridae because its uropod 3 bears subequal rami (Krapp-Schickel 2008).

Within Maeridae, three groups are recognized. The *Ceradocus* group is characterized by the inner plates of both maxillae being fully setose medially, the inner plate of maxilla 2 being widened and often triangular, the third article of the mandibular palp showing varying degrees of reduction, and the first article typically being distally elongate and pointed, forming a "knee" at this articulation (Krapp-Schickel 2009). The *Elasmopus* group is characterized by well-developed eyes, a notch or slit on the head cheek and a rounded to subacute anteroventral corner, a short to minute accessory flagellum, the third article of the maxillipedal palp with a distomedial flap, coxa 1 produced anteroventrally, pleonites and urosomites without dorsally serrate posterodistal margins, and the rami of uropod 3 never more than twice the length of the peduncle (Lowry and Hughes 2009). The *Maera* group is characterized by a three-articulate mandibular palp with article 3 straight, the inner plates of both maxillae apically setose, the medial margin of the inner plate of maxilla 2 sometimes bearing distal setae together with apical setae, and the medial margins of the inner plates of maxillae 1–2 often with feeble setae (Ariyama 2018). *Renomaera* gen. nov. cannot be placed in any of these three groups due to the following characters: eyes absent; head lacking a notch or slit; the inner plate of maxilla 1 bearing only one apical plumose seta, whereas the inner plate of maxilla 2 is strongly setose medially; the first article of the mandibular palp not pointed distally and the third article not falcate; the accessory flagellum elongate; coxa 1 not produced anteroventrally; a gill present on coxa 7; and the telson without apical setae (Krapp-Schickel 2009; Lowry and Hughes 2009; Corbari and Sorbe 2015; Ariyama 2018).

Another fifteen maerid genera were not assigned to the three groups above: *Anelasmopus* Oliveira, 1953 (monotypic, shallow water), *Animoceradocus* G. Karaman, 1984 (monotypic, shallow water), *Bathyceradocus* Pirlot, 1934 (five species, 330–7340 m depth, associated with sunken wood), *Ceradocoides* Nicholls, 1938 (monotypic, intertidal), *Ceradocopsis* Schellenberg, 1926 (seven species, shallow water, algal habitats), *Coxomaerella* G. Karaman, 1981 (monotypic, shallow water), *Cuniculomaera* Tandberg & Jażdżewska, 2024 (monotypic, 3416 m depth), *Elasmopoides* Stebbing, 1908 (monotypic, shallow water), *Jerbarnia* Croker, 1971 (four species, shallow water), *Maerella* Chevreux, 1911 (four species, shallow water), *Metaceradocoides* Birstein & N. Vinogradova, 1960 (monotypic, 7210–7230 m depth), *Papuadocus* Corbari & Sorbe, 2015 (monotypic, 500–580 m depth, associated with sunken wood), *Paraceradocus* Stebbing, 1899 (six species, shallow water), *Pseudelasmopus* Ledoyer, 1978 (two species, shallow water), and *Wimvadocus* Krapp-Schickel & Jarrett, 2000 (monotypic, with the holotype found in cod stomachs) (Stebbing 1908; Oliveira 1953; Birstein and Vinogradova 1960; Croker 1971; G. Karaman 1981, 1984; Andres 1984; Krapp-Schickel and Jarrett 2000; Krapp-Schickel 2008, 2009; Lowry and Hughes 2009; Corbari and Sorbe 2015; Hughes 2015; Ariyama 2018; Ariyama and Moritaki 2020; SOSA et al. 2024). *Renomaera* gen. nov. differs from all genera occurring in intertidal or shallow-water habitats by the absence of eyes, only the inner plates of maxilla 2 bearing long plumose setae, and the reduced inner and outer plates of the maxilliped (Nicholls 1938; Oliveira 1953; Croker 1971; G. Karaman 1981, 1984; Krapp-Schickel 2008; Hughes 2015).

Similar to the present new genus, species of five other genera – *Bathyceradocus*, *Cuniculomaera*,

Metaceradocoides, *Papuadocus*, and *Wimvadocus* – have been recorded from deep-sea or abyssal environments. *Renomaera* gen. nov. differs from these genera by the absence of a mandibular molar, the inner plate of maxilla 1 bearing only one apical plumose seta, reduced inner and outer plates of the maxilliped, the presence of a peduncular spur on uropod 1, and long plumose setae present on the inner ramus of uropod 3 (Pirlot 1934; Birstein and Vinogradova 1960; Krapp-Schickel and Jarrett 2000; Corbari and Sorbe 2015; SOSA et al. 2024).

The diagnosis of Maeridae should be amended as follows: mandible molar triturative or absent; uropod 3 inner ramus with or without long plumose setae (after Lowry and Myers 2013; Corbari and Sorbe 2015).

Renomaera patricki sp. nov.

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Material examined. ***Holotype.*** Western Pacific • one brooding female (with 13 intra-marsupial individuals), BL = 9.3 mm; a seamount located near the Mariana Trench (tentatively named M2 Seamount); 11°20'N, 139°17'E; depth 779.6 m; 15 Mar. 2016; MBM 288332.

Description. ***Body*** (Figs 2, 3) elongate and laterally compressed. Pleonites 1–3 (Figs 2, 3) not toothed on posterodorsal margin. Urosomite 1 with two teeth on posterodorsal margin medially. Urosomite 2 with one tooth on posterodorsal margin medially. Urosomite 3 with one lateral tooth. Epimera 1 and 2 with acute posterodistal corner, posterior margin sinuous and smooth. Epimera 3 with acute posterodistal corner, posterior margin concave and smooth.

Head (Figs 2, 3). Rostrum present. Eyes absent. Lateral cephalic lobe rounded: antennal sinus absent; anteroventral corner rounded. Antenna 1 longer than antenna 2; peduncle short, article 1 expanded, slightly longer than article 2, article 3 about 1/3 length of article 2; primary flagellum with 78 articles; accessory flagellum longer than peduncle, with 13 articles, article 1 slightly shorter than article 1 of primary flagellum. Antenna 2 peduncular article 4 subequal to article 5; flagellum with 31 articles.

Mouthparts (Fig. 3). Upper lip broader than long, bilobate. Mandible incisor well developed, with two large teeth, distal margin slightly serrated; right and left setal row with three and two robust setae, respectively and row of long simple setae; left lacinia mobilis similar to incisor heavily chitinous, distal margin with irregular teeth; right lacinia mobilis absent; molar absent; palp 3-articulate, article 1 shortest, with one seta near distal margin, article 2 longer and broader than article 3, posterior margin with long setae, article 3 straight, not falcate, distal half of posterior margin and tip with long setae. Lower lip inner

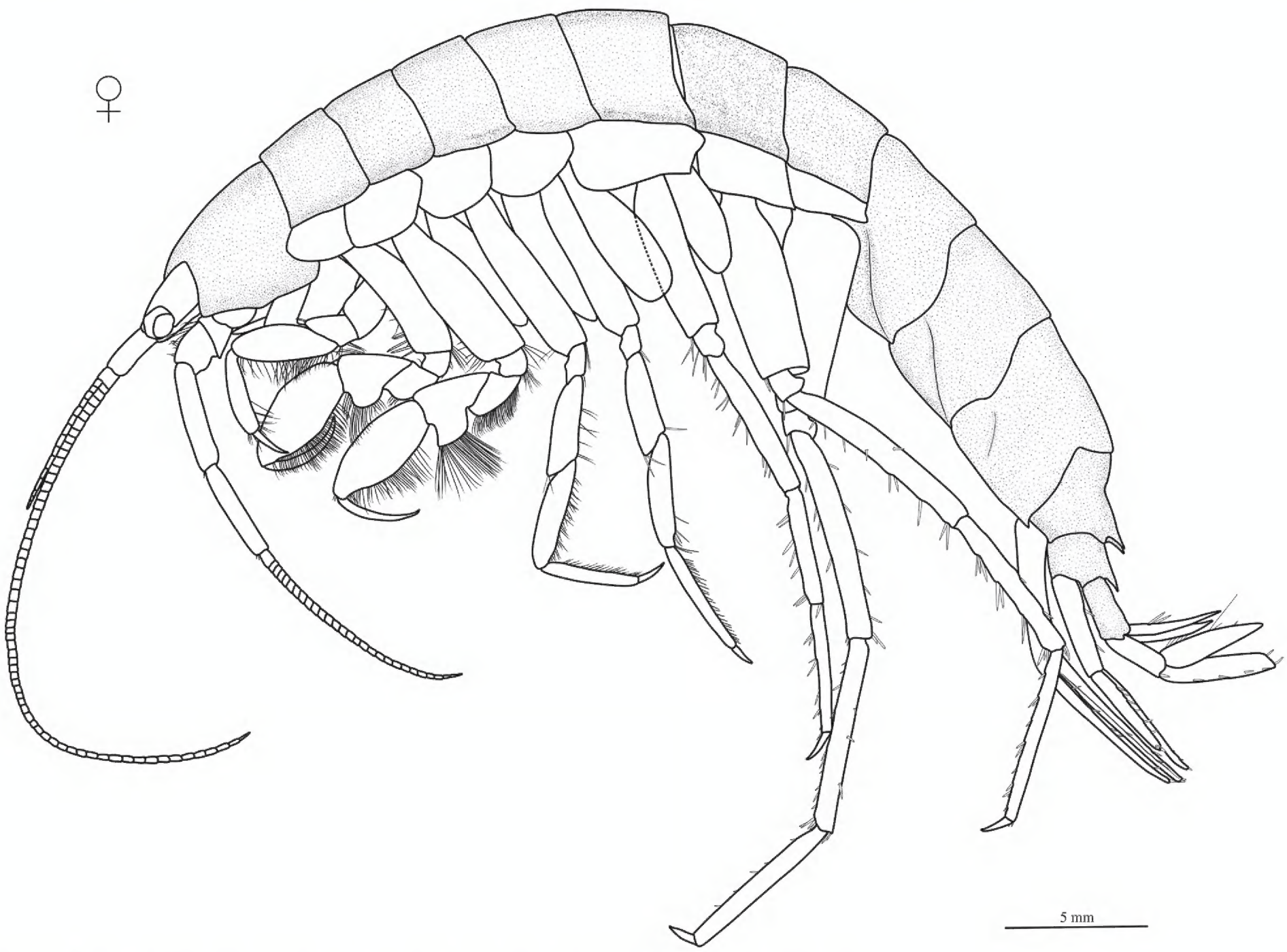

Figure 2. *Renomaera patricki* sp. nov., female holotype (MBM 288332), lateral view.

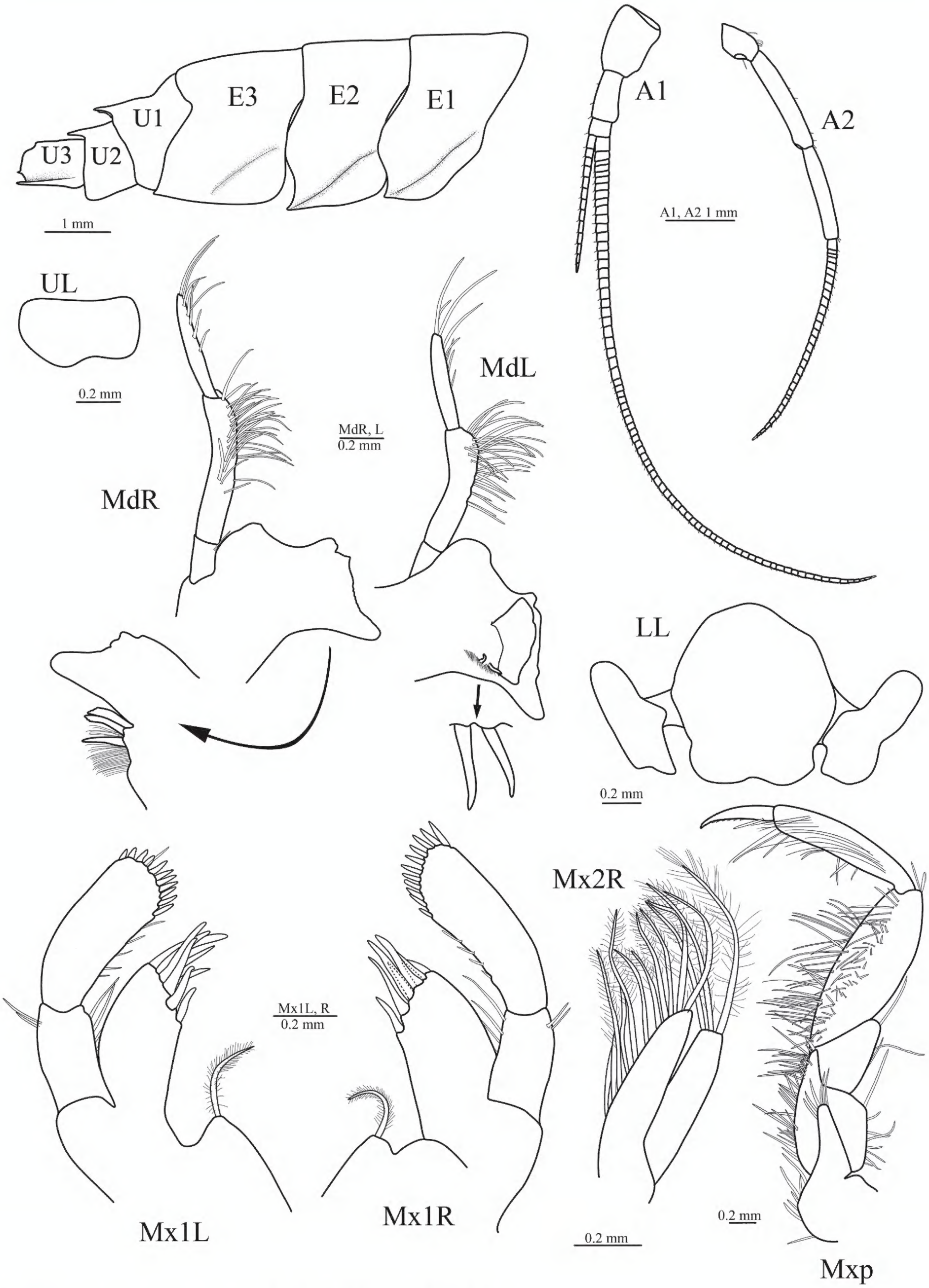

Figure 3. *Renomaera patricki* sp. nov., female holotype (MBM 288332).

lobe large, not lobate, rounded; outer lobes slender, apical margin bearing minute short setae. Maxilla 1 symmetrical; inner plate small, with one long apical plumose seta; outer plate with eight smooth setae; palp 2-articulate, article 2 longer than article 1, inner margin with 4–5 setae, distal margin with 11 robust setae. Maxilla 2 outer plate

shorter than inner one, only with three long plumose setae apically; inner plate with 11 long plumose setae on medial and distal margins. Maxilliped with inner plates short, triangular, with 6 setae distally; outer plates reduced, hardly reaching to distal margin of palp article 1, with setae on apical and medial margins; palp slender, article 2 subequal to article 3, with long setae facially, article 3 distinctly broader than article 2, with setae facially and on medial margin, article 4 shortest, lacking robust seta (nail), with minute setae on medial margin.

Gnathopods and pereopods (Figs 2, 4). Coxae 1–4 subrectangular, coxa 4 not excavate posteriorly. Coxae 5 and 6 not lobate. Coxa 7 smaller than coxae 5 and 6, subrectangular. Coxal gills present on pereopods 2–7. Oostegites on pereonites 2–5.

Gnathopods 1–2 similar in shape, subchelate, but gnathopod 2 slightly longer. Gnathopod 1 basis with short setae on anterior and posterior margins; ischium posterior margin bearing several setae distally; merus shorter than carpus, posterior margin bearing row of setae; carpus shorter than propodus, posterior margin with rounded lobe bearing long setae, anterior margin bearing a group of setae distally; propodus sub-ovate, twice longer than wide, palmar margin obliquely convex, with dense robust setae; dactylus 7/10 length of propodus, curved. Gnathopod 2 symmetrical; basis longer than that of gnathopod 1, posterior margin bearing dense short setae; ischium to carpus similar to gnathopod 1; propodus slender, more than twice longer than wide, palmar margin obliquely convex, with dense robust setae; dactylus 4/5 the length of propodus, curved. Pereopod 3 slightly shorter than pereopod 4, basis linear, anterior margin bearing setae; merus slightly shorter than carpus, posterior margin bearing setae, anterior margin bearing group of setae distally; carpus shorter than propodus, posterior margin bearing setae; propodus slender, posterior margin bearing dense setae; dactylus slender, simple. Pereopods 5–7 slightly increasing in length, basis of pereopods 5 linear, those of pereopods 6 and 7 slightly expanded, subrectangular, not serrate; merus of pereopods 5 and 6 longer than carpus and propodus, carpus shorter than propodus, merus of pereopod 7 subequal to propodus, longer than carpus; dactylus slender, simple.

Uropods and telson (Figs 2, 4). Uropod 1 slightly extending beyond the end of uropod 2; peduncle shorter than rami, with spur on ventral margin, reaching to 1/3 length of inner ramus, with six robust setae; inner ramus subequal to outer ramus, with 11 marginal and two distal robust setae; outer ramus with ten marginal and one distal robust setae. Uropod 2 peduncle shorter than rami, with inner margin produced as acute tooth distally, dorsal surface bearing seven robust setae; inner ramus longer than outer one, with ten marginal and one distal robust setae; outer ramus with seven marginal and one distal robust setae. Uropod 3 with peduncle much shorter than rami, peduncle with one dorsal and two ventral robust setae; inner ramus with six marginal and two distal robust setae, inner margin serrated, bearing three long plumose setae; outer ramus slightly longer than inner one, with five marginal and two distal robust setae, inner margin serrated. Telson linguiform, cleft about 70% of its length; each lobe bilobated apically; dorsal surface of each lobe bearing five robust setae in two rows.

Etymology. This species is named after Patrick Star from the cartoon "SpongeBob SquarePants." Because Patrick is SpongeBob's best friend, and this new species was collected in association with a sponge.

Distribution. Presently known only from a seamount located near the Mariana Trench at a depth of 779.6 m.

Remarks. See remarks for the genus.

Molecular data analysis

Based on the first data set, the phylogenetic trees produced by the BI and ML analyses showed limited congruence, but both strongly rejected the monophyly of the family Maeridae (Fig. 5). Both ML and BI tree topologies indicated that *Renomaera patricki* gen. et sp. nov. clustered with four maerid species, including *Maera danae* (Stimpson, 1853), a species from the type genus, with strong support (BP = 89% and PP = 0.94). In the BI analysis, *Linguimaera* sp., a member of the *Maera* group, was placed as a sister group to the remaining maerid species and to species within the other five families, with moderate support (PP = 0.63). In contrast, the ML tree grouped *Linguimaera* sp. with two *Elasmopus* group members, *Elasmopus nkjaf* Nakamura, Nakano, Ota & Tomikawa, 2019, and *Mallacoota insignis* (Chevreux, 1901), with moderate support (BP = 70.7%). The deep-sea maerid species *Bathyceradocus hawkingi* Jażdżewska & Ziemkiewicz, 2019 clustered with another maerid, *Papuadocus blodiwai* Corbari & Sorbe, 2015 (reported from depths of 500–800 m), and one nuuanuid species in the BI analysis, albeit with weak support. However, in the ML analysis, *B. hawkingi* formed a sister group to species from the other four families, with strong support (BP = 85.6%). Species from the other three families (Metacrangonyctidae Boutin & Messouli, 1988, Melitidae, and Eriopisidae Lowry & Myers, 2013) each formed its own strongly supported clade in both the ML and BI analyses.

Based on the second data set, the two inference methods (ML and BI) resulted in generally congruent topologies (Fig. 6). As in the first data set, *Renomaera patricki* gen. et sp. nov. clustered with the same four maerid species, although here as a sister group and with weaker support (BP = 64.2% and PP = 0.44). In contrast to the first data set, *Linguimaera* sp. was recovered as a sister group to these five species. *B. hawkingi* also formed a sister group to species from the other four families, with strong support (BP = 89.4% and PP = 0.89). Species from the three other families (Metacrangonyctidae, Melitidae, and Eriopisidae) each also formed a strongly supported clade in both analyses.

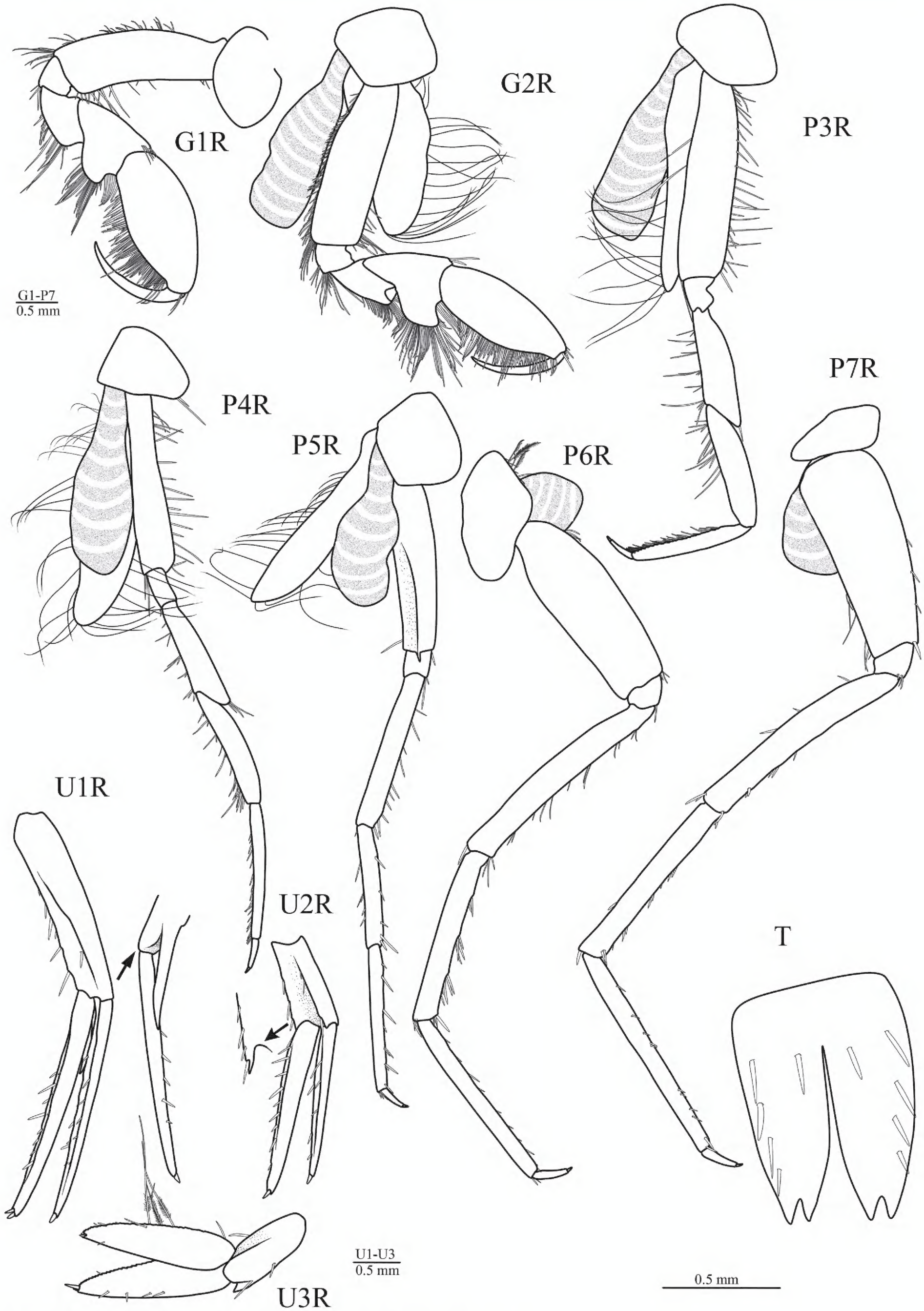

Figure 4. *Renomaera patricki* sp. nov., female holotype (MBM 288332).

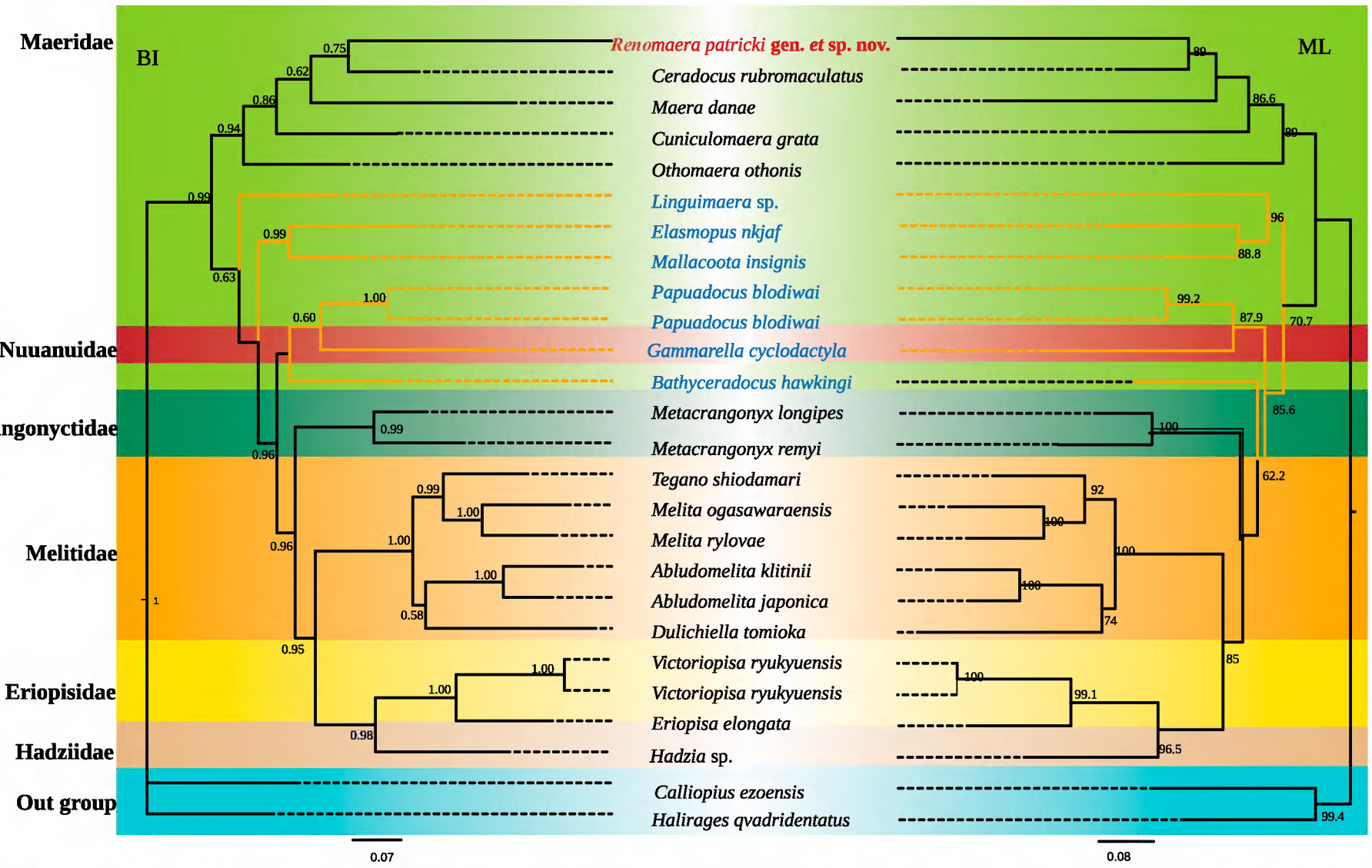

Figure 5. Left: Bayesian inference (BI) and right: maximum likelihood (ML) trees of the superfamily Hadzioidea, based on combined sequences of H3, COI, and 28S.

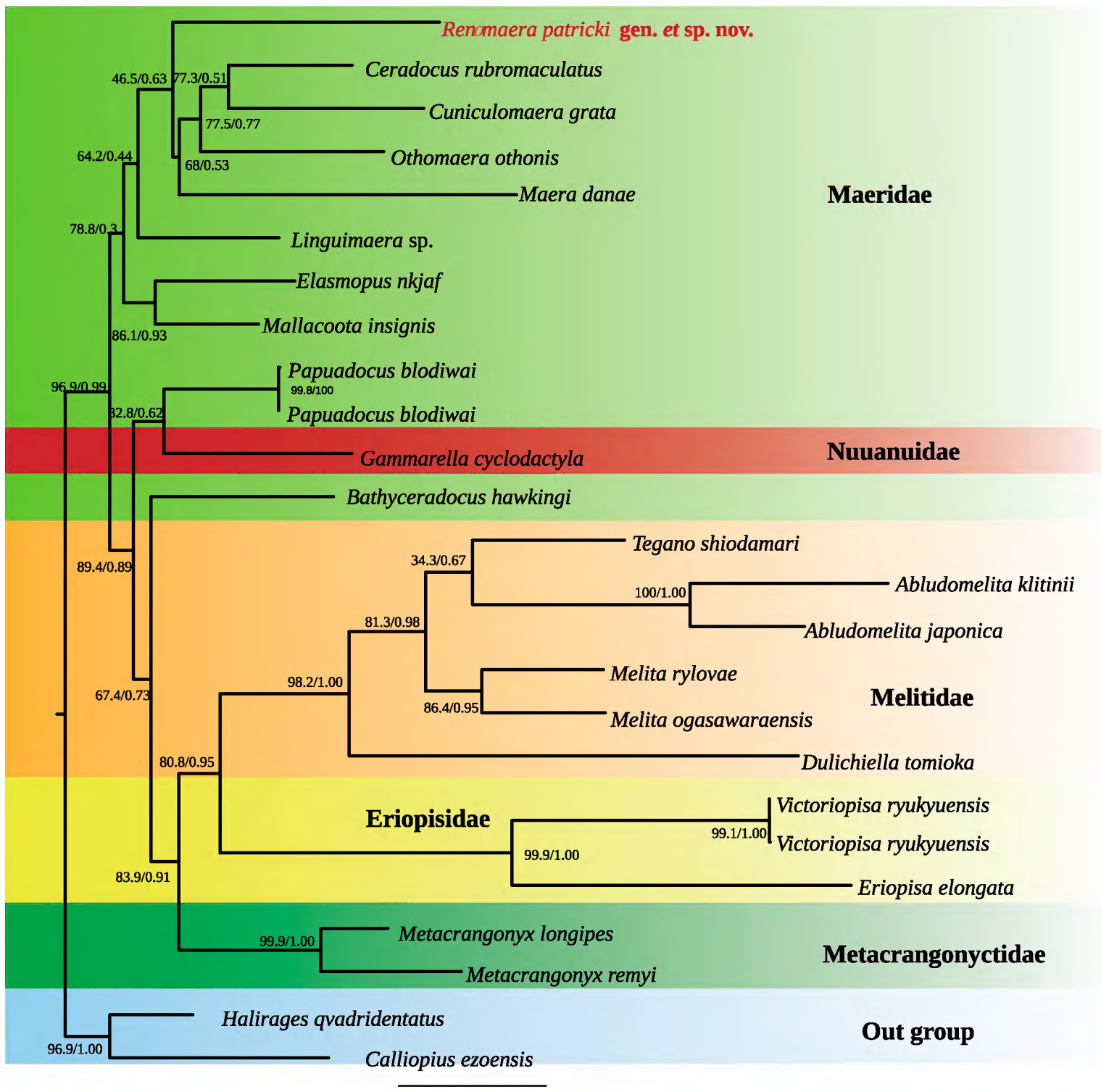

Figure 6. Phylogenetic tree of the superfamily Hadzioidea, with taxa resolved based on the combined data set of two genes (COI and H3).

The monophyly of Nuuanuidae could not be verified because only one species was included in the analyses; however, it was suggested to be sister to the maerid species *Papuadocus blodiwai*, with high support inferred from analyses based on both data sets.

Discussion

The results of the present study clarified *Renomaera patricki* gen. et sp. nov. as closely related to members of Maeridae, although the monophyly of the family itself was not supported. This is the first time that a deep-sea maerid species has been found associated with a sponge (*Semperella* sp.), whereas other deep-sea maerid species (representing at least 15 genera) have been recorded from muddy substrates or in association with sunken wood (Schellenberg 1926; Barnard 1932; Birstein and Vinogradova 1960; Lowry and Bullock 1976; Mukai 1979; Andres 1984; Krapp-Schickel and Vader 2013; Corbari and Sorbe 2015; Hughes 2016; SOSA et al. 2024). Similar to *Huonella huonensis* Hughes, 2016, *R. patricki* gen. et sp. nov. was reported from seamounts in the tropical western Pacific, where it harbors vibrant biodiversity (Morato et al. 2010).

The family Maeridae is separated from Melitidae based on uropod 3 having subequal rami (Krapp-Schickel 2008; Lowry and Myers 2013). However, the monophyly of Maeridae has not been supported by previous phylogenetic analyses based on a single 18S ribosomal DNA gene (Englisch et al. 2003). In those analyses, *Paraceradocus gibber* Andres, 1984, and *Quadrimaera inaequipes* (A. Costa in Hope, 1851) (formerly classified in *Maera*; see Krapp-Schickel and Ruffo 2000) were not clustered together. Our analyses also rejected the monophyly of Maeridae but supported the monophyly of Metacrangonyctidae, Melitidae, and Eriopisidae.

The *Maera* group is characterized by the straight third article of the mandibular palp (Krapp-Schickel 2008; Ariyama 2018) and contains 20 genera (Ariyama 2018; SOSA et al. 2024). In our analyses, the *Maera* group was represented by four species (*Cuniculomaera grata*, *Othomaera othonis*, *Maera danae*, and *Linguimaera* sp.). The monophyly of the *Maera* group was not supported herein (Figs 5, 6). The *Elasmopus* group is characterized by well-developed eyes and a short to minute accessory flagellum (Lowry and Hughes 2009) and was represented by *Elasmopus nkjaf* and *Mallacoota insignis* in the present study. Our analyses supported the monophyly of the *Elasmopus* group. The monophyly of the *Ceradocus* group, characterized by a mandibular palp with a pointed first article and a reduced third article and a serrated epimeral plate 3, could not be verified because only one species (*Ceradocus rubromaculatus*) was included in our analyses. As the superfamily Hadzioidea is large, relatively few species and genera were included in the present study. Therefore, a comprehensive understanding of the systematic relationships among families and groups within Hadzioidea will require further taxonomic and molecular data sampling.

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Supplementary material 1

All sequences were deposited in GenBank

Authors: Zhong-Li Sha, Yan-Rong Wang
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